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THE ADULT CYCAD TRUNK

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 146

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(WITH TWENTY FIGURES)

The structure and development of the cycad seedling is fairly well known in all the genera, and in *Dioon*, *Ceratozamia*, and *Microcycas* recent investigations have been particularly thorough; but some features of the adult trunk have hitherto escaped observation, doubtless because such material is so difficult to obtain. As a matter of fact, most of the descriptions are based upon dead conservatory plants which had begun to decay and so had become worthless as ornamental specimens.

Historical

As early as 1829, BRONGNIART (**1**) described the stem of *Cycas revoluta*, and showed clearly that, in spite of the external habit, the woody structure was not at all related to that of palms, but resembled the wood of dicotyls, the principal difference being that *Cycas* had no bast or growth rings.

VON MOHL (**2**) studied a specimen of "*Zamia latifolia*" (*Encephalartos*) 1.5 meters in height, and also a section of a large trunk of *Cycas revoluta*. He recognized the bast and described the histological characters of the wood, which he found to resemble that of dicotyls, except that it lacked true vessels. In the pith he found bundles like those of many cacti. There were no growth rings.

The excellent work of METTENIUS (3), published in 1861, deals with *Cycas revoluta*, *Encephalartos horridus*, *Dioon edule*, and *Zamia muricata*. The course and structure of leaf traces are described in detail, and spiral vessels are noted for the first time, these having escaped the observation of previous investigators, probably because in mature stems they are lacking next the pith, where one might expect to find them. He saw bundles in the pith of *Dioon* and correctly interpreted them as belonging to the vascular system of the peduncle.

SOLMS-LAUBACH (4) traced the vascular supply of the peduncles in *Stangeria paradoxa* and *Ceratozamia mexicana*, and also noted the formation of phellogen in the leaf bases.

In his *Histologische Beiträge* III, STRASBURGER (5) describes the histological structure of a large trunk of *Cycas circinalis*, and gives a critical discussion of the literature.

In 1896, WORSDELL (6) made a thorough investigation of a large trunk of *Macrozamia Fraseri*. This form has a well-developed system of vascular bundles in the pith, described as not being connected in any way with peduncles. There are also concentric zones of wood, as in *Cycas*, and these, WORSDELL (6) believes, are remnants of some ancient structure which consisted of rings or layers of concentric vascular strands. To him the structure recalls that of the *Medullosa* stem.

From these accounts we get our conventional idea of the cycad stem, with its armor of leaf bases, thick cortex, narrow zone of wood, large pith, numerous medullary rays, and no growth rings.

Investigation

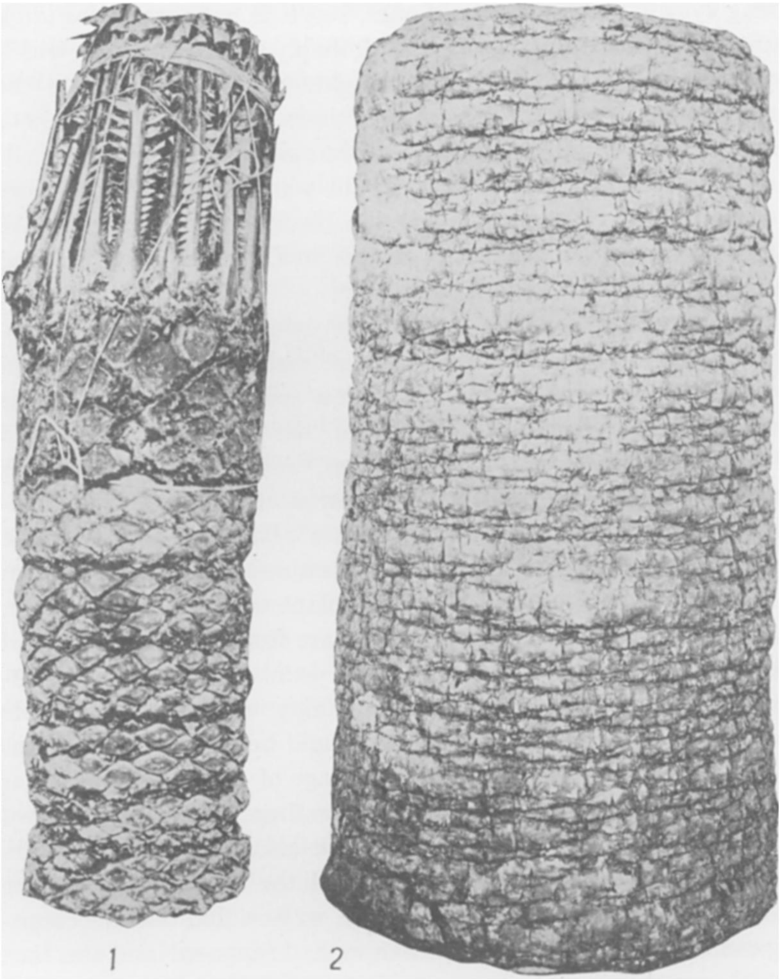
In September 1910 I was able to study in the field the adult trunks of *Dioon edule* and *D. spinulosum*, the study being facilitated by the active encouragement of Gov. TEODORO A. DEHESA, of the state of Vera Cruz. The field study was supplemented by notes and material from Mr. ALEXANDER M. GAW, of the Bureau of Information, Jalapa, state of Vera Cruz. Abundant material of *Dioon spinulosum*, accompanied by notes, was sent to me by Mr. J. C. DENNIS, superintendent of the Hacienda de Joliet, near Tierra Blanca, but in the state of Oaxaca. I am glad to acknowledge my indebtedness to these gentlemen, for without their cooperation the investigation of such inaccessible material would have been impossible.

MACROSCOPIC STRUCTURE

The conventional account of the trunk is doubtless true for all young cycads and for most old ones, but it is not correct for large plants of *Dioon spinulosum*, and probably not for others which have attained any considerable height. In *D. spinulosum* the large amount of wood, the zone sometimes reaching a thickness of 10 cm., first attracted my attention, but since material was available, it seemed desirable to examine the whole trunk. Plants were studied both at Tuxtepec and at the Hacienda de Joliet, but the following account, whenever it relates to *D. spinulosum*, is based upon material from the latter locality.

AGE.—As mentioned in a previous paper (**7**), the trunk sometimes reaches a height of more than 16 meters. From the crown to the base the trunk is marked with a series of ribs due to the alternation of foliage and scale leaves, the constrictions between ribs corresponding to the scale leaves, and the ribs themselves being the larger leaf bases of the crowns of foliage leaves. Obviously, the number of crowns which a plant has borne can be determined by counting the ribs, and, assuming that a new crown is produced each year, the age of the plant would then be known. But it is not certain that new crowns are formed every year, and whether the interval is regularly two years remains to be determined. At any rate, an estimate making the number of years correspond to the number of crowns would be extremely conservative. In our previous account (**7**) the age of the tallest specimens was estimated at about 400 years, the estimate assuming a crown to be produced every other year. It was also stated that the scars are so obscure on the lower portions of the trunk that accurate counting is difficult. While this is true, we now find that the counting can be carried much farther than we had supposed, and also that the obscure ribs formed by successive crowns are very much closer together in the lower than in the upper portion of the trunk. The difference between the upper and lower portions of a trunk 6 meters in height is shown in figs. 1 and 2, the lower portion being taken

30 cm. above the surface of the rock upon which the plant was growing. The foliage display practically always consists of two successive crowns, the leaves of the lower standing transversely or beginning to droop, while those of the latest crown are more erect, but the two nevertheless presenting the appearance of a single



FIGS. 1, 2.—*Dioon spinulosum:* fig. 1, upper part of a trunk 6 meters in height; the latest crown is tied with the string, the next crown below has been cut away with a machete, and the leaves of the 6 crowns below this have fallen off naturally; ×$\frac{1}{6}$; fig. 2, lower part of same trunk, showing scars of 21 crowns; ×$\frac{1}{5}$.

crown. In fig. 1 the latest crown is tied to protect the bud, and the leaves of the crown below have been cut off. With this explanation, it will be seen that the upper portion has borne 8 crowns. The lower portion has borne 21 crowns, of which 6 or 7 toward the top are easily counted, while the rest are increasingly indistinct. How many crowns were borne by the intervening piece, about 4 meters in length, and also by the stump, is not known, but 100 crowns would be a very low estimate, and the plant would be more than 100 years old even if a new crown were produced every year.

ARMOR.—In some forms, like *Dioon edule* and *Encephalartos Altensteinii*, the armor of leaf bases is so persistent that each leaf base is distinguishable even in the lower portion of the trunk, while in *Dioon spinulosum* and others the leaf bases become indistinguishable in the lower portion of old trunks.

In *Dioon edule*, below the two green crowns constituting the foliage display and appearing as a single crown, is a crown represented by decaying midribs from which most of the leaflets have fallen, and below this will be found one or more crowns represented by irregular jagged stumps, several centimeters in length, and it is only below these that one finds the smoothly cut off bases. The reason is easily determined. As in annually deciduous dicotyls, an abscission layer of phellogen is developed, but at so late a period that only a decayed stump of midrib remains to be cut off. After the stump has fallen, a new phellogen appears a little deeper than the first, and then another, so that successive phellogens keep scaling off the outer surface, even in forms with such persistent leaf bases as *Dioon edule*. At Chavarrillo, where this species is most abundant, the trunk is often damaged by fire. In such cases, where the entire armor may be destroyed, an extensive phellogen appears in the cortex, the meristematic layer sometimes reaching a width of several millimeters, and in this way a smooth protective covering is built up.

In *Dioon spinulosum* the phellogens are more vigorous, and successive layers are scaled off until the leaf bases in the lower portion of old trunks become indistinguishable, and even the ribs due to the alternation of scale and foliage leaves become obscure. We have never seen a specimen of *Dioon* from which all of the armor had scaled off, except in case of injury.

CORTEX.—The cortex of a large plant grows rapidly for a few years, and then during the long life of the plant grows very little. In a 6-meter specimen of *Dioon spinulosum*, at a distance of 15 cm. below the apex, the width of the zone of cortex, measured from the outer border of the phloem to the beginning of the leaf base region, was 1–1.5 cm.; while the width of the cortex near the base of the stem, where the tissues were at least 100 years older, had increased only to 1.5 or 2 cm.

Except in cases of injury, there are no meristematic regions in the cortex, *Dioon* being strictly monoxylic, and there is no growth by a phellogen at the periphery, the phellogen layers being confined to the leaf base region and not reaching the cortex itself. In forms which lose their armor through the vigorous activity of successive phellogens, the cortex itself is invaded, but in such cases the invading phellogen adds as much or more than it cuts off, and the stem may even increase in diameter.

The cortex is traversed by numerous leaf traces, some of them direct and others forming the characteristic girdle. There are also numerous mucilage canals and cavities, some of them following the course of the bundles, but most of them being independent. Crystals of calcium oxalate are numerous, and tannin cells are so abundant that a freshly cut stem changes color in a few minutes.

AMOUNT OF XYLEM.—The cycad stem has always been described as having a large pith and cortex, with a small zone of wood between them.

According to BRONGNIART (1), a specimen of *Zamia latifolia* (doubtless an *Encephalartos*), 1.5 meters in height and 20.5 cm. in diameter, had a pith 7.5 cm. in diameter, surrounded by a vascular zone 6 mm. in width, the xylem and phloem being of about equal thickness; beyond the phloem was a narrow cortex about 8 mm. in width, followed by a broad zone of leaf bases 5 cm. in width.

A few measurements which we have made recently are given below, all measurements being made at approximately the greatest diameter of the plant.

A plant of *Ceratozamia mexicana*, collected about 10 kilometers north of Jalapa, had a trunk 30 cm. high and 15 cm. in diameter. The pith, 5.7 cm. in diameter, was surrounded by a zone of zylem 3 mm. wide, with phloem 2 mm. wide, beyond which was the cortex 1.5 cm. wide, and surrounded by a heavy armor of leaf bases.

A mature plant of *Zamia floridana*, with a stem 15 cm. in height and 6 cm. in diameter, had a pith 1.3 cm. in diameter, the zones of xylem and phloem each measuring 2 mm. in width, and the cortex about 2 cm. in width. The entire armor had disappeared, and a comparatively regular phellogen had become established in the cortex.

A specimen of *Dioon edule* at Chavarrillo, with a trunk about 60 cm. in height and 21 cm. in diameter, had a pith 8.7 cm. in diameter, the zones of xylem and phloem each measuring 5 mm. in width, the cortex 2 cm., and the leaf bases 3.6 cm. A taller specimen, about 1 meter in height, but with the same diameter, had the following dimensions: diameter of pith, 6.9 cm.; width of xylem, 1.5 cm.; width of phloem, 8 mm.; width of cortex, 3.2 cm.; width of leaf base region, about 1.5 cm.

These measurements may be regarded as typical of most monoxylic trunks. The mount of wood in polyxylic trunks, though somewhat greater, is still so scanty that no exception to the conventional description has been necessary.

Naturally, it was with considerable surprise that I noted, in the Tierra Blanca region, trunks of *Dioon spinulosum* with zones of wood 4, 6, and even 10 cm. in width. A specimen 6 meters in height, and 33 cm. in diameter at a distance of 30 cm. above the rock on which it was growing, had a zone of wood 10 cm. in width. The phloem was 1.4 cm. in width, the cortex 2.5 cm., and the armor near the base of the plant, where it had been greatly reduced, only 0.5 to 1 cm. The pith at a distance of 60 cm. below the apex was 8 cm. in diameter, and from this point to the base of the plant its diameter was uniform. What the extent of the wood in a specimen 15 or 16 meters in height might be, remains to be determined.

The numerous large medullary rays reaching from the pith to the cortex are a conspicuous feature of the transverse section (fig. 3). Besides the large rays there are much more numerous small ones. Both kinds of rays have a comparatively slight longitudinal extent. Each large medullary ray contains a leaf trace bundle, but the small rays are in no way connected with bundles.

GROWTH RINGS.—*Dioon spinulosum* has well-developed growth rings, a feature which, so far as I know, has not been described for any cycad. These rings are conspicuous in the upper part of the trunk, and can be recognized even in the lower portions of old plants (figs. 3 and 19). That the rings are growth rings, and that they have approximately the same structure as the annual rings of dicotyls, is obvious from a glance at a transverse section; but that they are annual rings is doubtful even in *Dioon spinulosum;* and in *D. edule,* where the rings are equally conspicuous, it is absolutely certain that they are not formed annually.

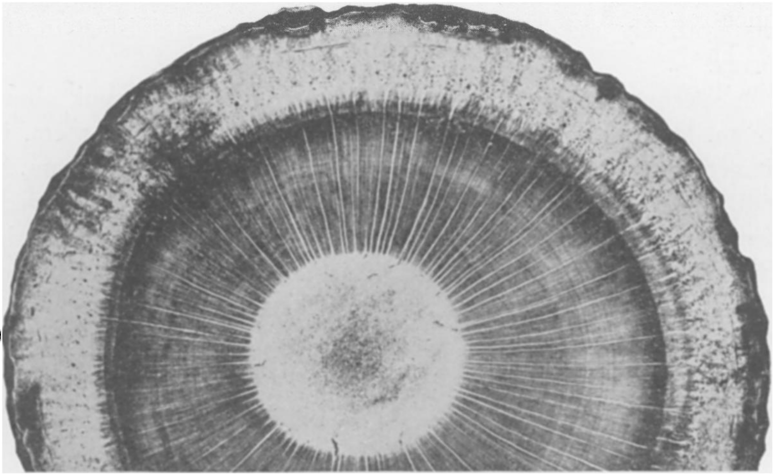


FIG. 3.—*Dioon spinulosum:* transverse section of lower part of the piece shown in fig. 2; note the large and small medullary rays, the growth rings, and the large amount of phloem; ×½.

A transverse section of the 6-meter plant of *Dioon spinulosum,* already mentioned, at the level of the third crown from the apex, showed four growth rings. This piece had borne one cone. A section of the same plant at the level of the eighth crown below the apex showed 13 growth rings. During the formation of the nine crowns the plant had produced at least 8 cones.

The number of rings, counted 30 cm. above the ground in the 6-meter specimen, was about 150. The number of crowns, at a very low estimate, was about 100. Any estimate of the number of cones would necessarily be very uncertain, the only data being that the first cone was borne when the plant was 1 meter in height, and that a piece 25 cm. in length, taken near the top of the plant, had borne 6 cones. Estimated only upon this data, the number of cones would have been more than 100, but the estimate is doubtless much too high, because ovulate cones are comparatively infrequent on small plants.

The number of rings, then, does not correspond exactly to either the number of crowns or the number of cones, or to the number of both combined. It is certain that in some seasons a plant produces a crown of leaves but no cone; and that it may produce a cone and no leaves; and, further, that it may produce both a new crown and a cone the same season, or it may fail to produce either a crown or a cone. It is quite probable that when either a crown or a cone is produced, a ring is formed, and that when both a crown and a cone are formed the same season, only one ring is produced.

We are inclined to believe that a period of vigorous growth, which would result in the formation of a new crown or cone, would produce also a growth ring, and that seasons which pass without the formation of a crown or a cone would not be marked by growth rings, the mere alternation of rainy and dry seasons not being sufficient for the formation of a ring in *Dioon*. If the number of rings should correspond somewhat approximately to the number of seasons, we should regard the correspondence as a coincidence, the crown and cone production being the determining factor. Of course, it is well known that dicotyls in such localities have seasonal growth rings.

In *Dioon edule* the growth rings present a very different problem, for it is certain that they correspond to neither the number of crowns, number of cones, nor number of seasons. At Chavarrillo, a plant 60 cm. in height and 20 cm. in diameter showed, in a transverse section near the base, a zone of wood 15 mm. in width. The number of rings was about 20, but the age of the plant, at a very conservative estimate, could not have been less than 100 years, nor the number of crowns less than 50, so that whatever the factor may be which produces the ring, it must appear at widely separated intervals. The trunk is obscurely ribbed, but the ribs do not correspond to the number of crowns, many crowns being represented in each rib. It is possible that these ribs are due to the resting periods during which neither crowns nor cones are produced. The number of rings may correspond to the number of these resting periods. It is possible that such resting periods may result in the formation of new zones of wood in polyxylic stems, like *Cycas revoluta*, and only in the formation of rings in *Dioon edule*. In either case, it would require time and some vandalism to secure evidence.

CONE DOMES.—Vascular bundles in the pith have doubtless been seen by everyone who has cut a section of any mature cycad stem, but METTENIUS (3), studying *Dioon edule*, was the first to interpret these bundles as the vascular system of the cones. Later, SOLMS-LAUBACH (4) made a more thorough study of the pith bundles in *Ceratozamia*, and showed conclusively that the cycad trunk is a sympodium. Still later, the mode of development of the sympodium was described by Miss F. GRACE SMITH (8), who studied the origin of young cones and stem apices in *Zamia floridana*.

We have studied the pith bundles in *Dioon spinulosum*, *D. edule*, and *Zamia floridana*. In longitudinal sections of the stem, the bundles are in the form of a convex diaphragm, but since they really form a dome with the peduncle of the cone at its apex, we shall call the system of bundles a *cone dome*.

The longitudinal section shown in fig. 4 contains five cone domes, the second of which, counting from the top, is cut through the axis of the peduncle, and the third and fifth show clearly the position of the peduncle, and the other two indicate its approximate location by a thickening of the bundles. In *Zamia floridana* the appearance is similar, but in *Dioon edule*, on account of the very slow growth, a single transverse section may show parts of as many as three cone domes.

In transverse section the cone dome appears as a circle of vascular bundles more or less eccentric if cut near the peduncle, but concentric near the stele (fig. 5).

As soon as a cone begins to develop, a new meristem appears very close to the peduncle, and this new meristem may form successive crowns of leaves, but sooner or later it becomes transformed into a cone, which is really only a highly modified crown of leaves terminating the growth of its axis. The process is then repeated. An instructive view of this phase is seen in fig. 6. A little to the right of the center is the peduncle of a large ovulate cone, and at its left is the new growing point which has produced a crown of foliage

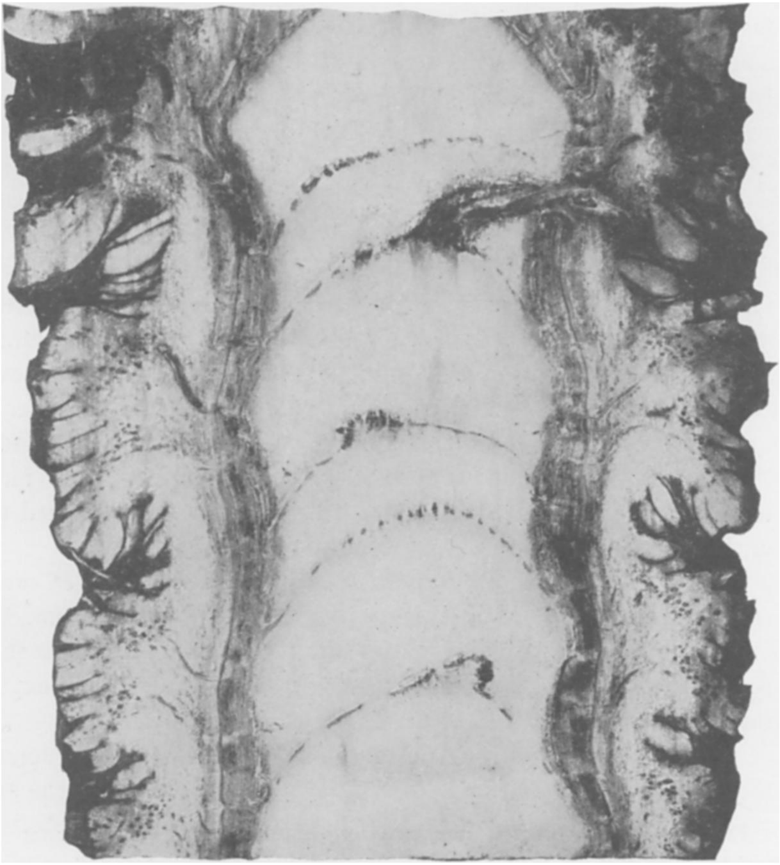


FIG. 4.—*Dioon spinulosum:* longitudinal section near the top of the piece shown in fig. 1; note 5 cone domes and, at the tip, a part of another; three ribs and parts of two more are shown; between the ribs are scale leaves; ×½.

eaves, and a crown of scale leaves appearing as a whitish triangular cluster in the figure, while the growing point itself is becoming transformed into a cone, a fact evidenced, as yet, only by a slight elongation, the point, while producing only vegetative leaves,

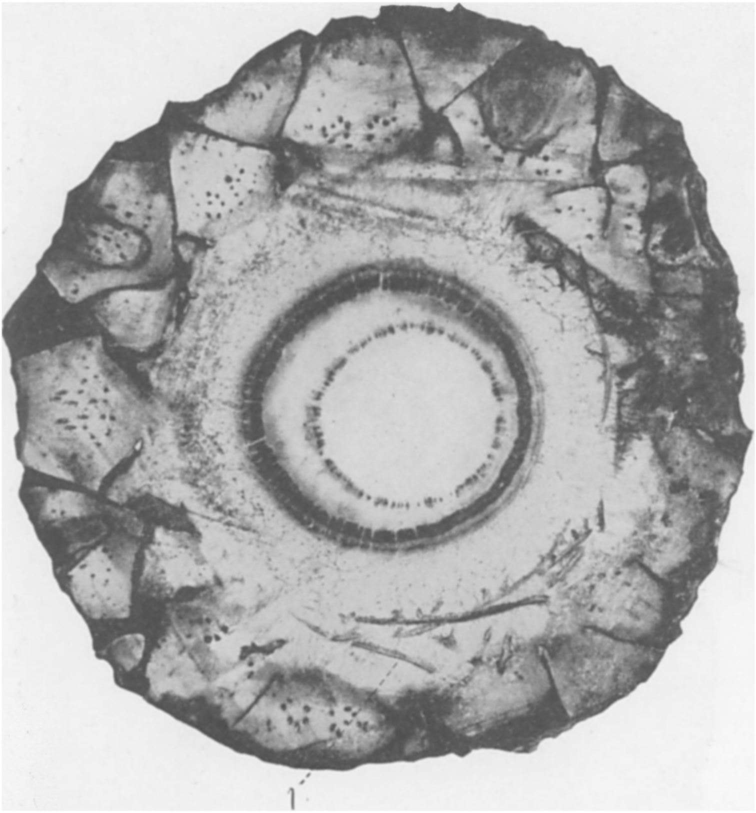


FIG. 5.—*Dioon spinulosum:* transverse section at about the level of the top of fig. 4; the innermost ring is the cone dome; beyond this is the vascular cylinder, with the xylem (quite dark) and the phloem (much lighter) about equal in width; the girdle leaf traces (*l*) are prominent; ×½.

being convex or at most hemispherical. Young cones of *Zamia* also may be distinguished from vegetative growing points, even before any appearance of sporophylls, by the elongation.

As the new apex develops, the old peduncle is pushed aside, new tissue gradually surrounds its base, and finally whatever remains of the old peduncle is covered over, somewhat as in the case of a dead branch of a dicotyl. The apex of the cycad stem is remarkably broad and flat, a feature which expedites the burying of the peduncle by the new tissue (fig. 6).

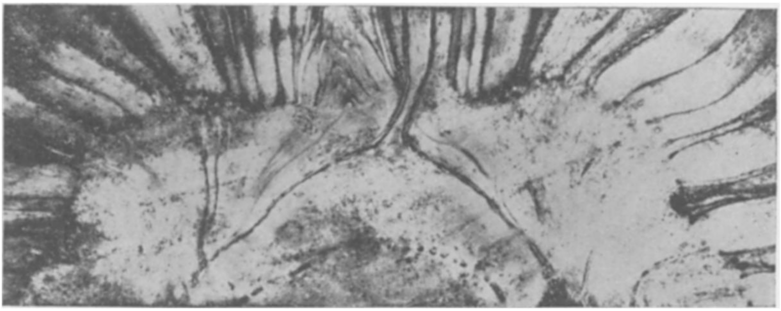


FIG. 6.—*Dioon edule:* longitudinal section of the apex of a large trunk, showing three cone domes, the lowest with bundles in transverse section, the middle one with bundles going to the peduncle of a large cone, and the upper terminating in the latest apex; ×⅔.

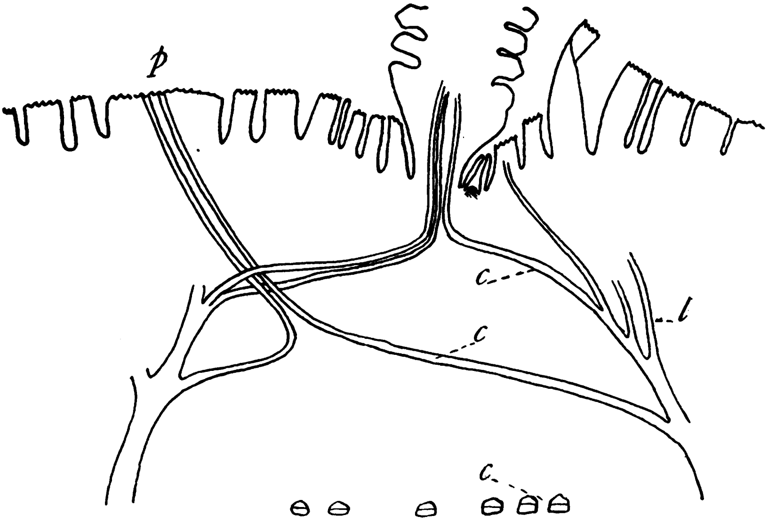
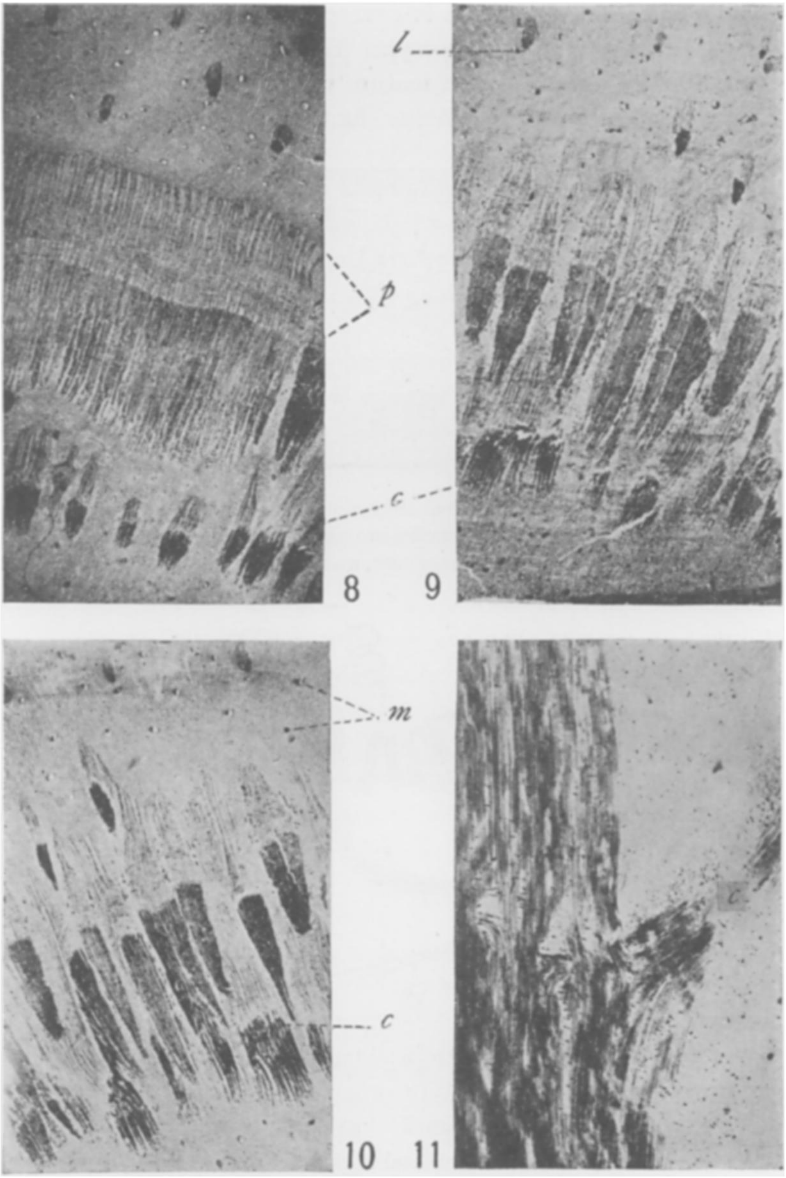


FIG. 7.—*Zamia floridana:* longitudinal section of apex of a large plant, showing three cone domes (*c*), the lower with bundles in transverse section, the middle with bundles running to the peduncle (*p*) of a mature cone, and the upper with bundles running to a young cone; the new growing point is at the right of the young cone; several leaf traces (*l*) are shown; ×3.



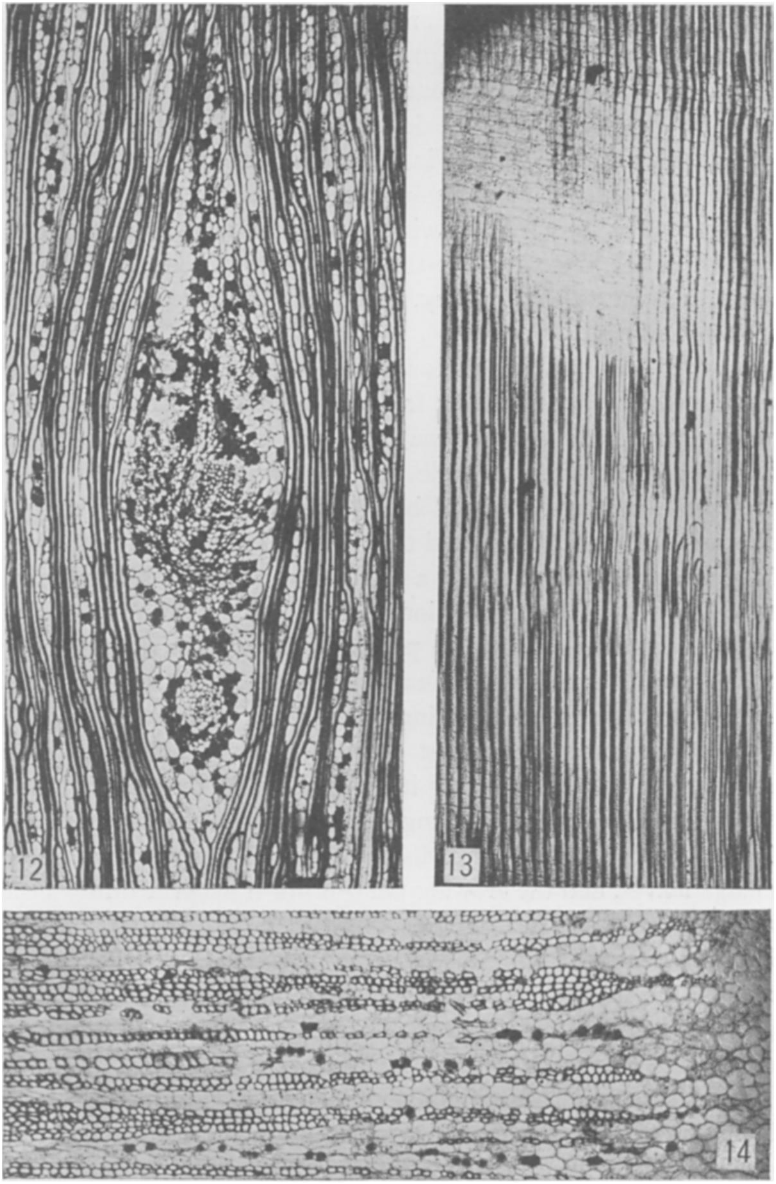
FIGS. 8–11.—*Dioon spinulosum:* *c*, cone domes; *m*, mucilage ducts; *l*, leaf traces; *p*, phloem; fig. 8, cone dome still separated from the main body of the stele; fig. 9, section at the union of cone dome and main body of stele; fig. 10, slightly more intimate union; fig. 11, longitudinal view of cone dome at point of union with main body of stele; all ×5.

The vascular connections are rather complex. Naturally, each cone dome must, at some point, surround the apex of the preceding cone dome. The general course of the bundles may be seen in fig. 7, which shows three cone domes, the lowest shown in transverse section, the next terminating in the base of an old peduncle, and the upper one passing into a young cone, while at the right of the young cone is the new growing point. It is evident from this figure and the preceding one that the traces of foliage leaves first touch the stele at its periphery, while the bundles of the cone domes are on the inside.

As long as the new dome is separated from the rest of the vascular tissue by a zone of pith, a transverse section looks like a section of a polyxylic stem, except that the smaller zone of vascular tissue is inside (fig. 8); but a little farther down, a transverse section presents a confused array of bundles (figs. 9 and 10). After the bundles of the cone dome and those of the previously formed wood have become arranged into a fairly regular zone, a cambium is established, and the formation of secondary xylem and phloem begins. In uniting with the previously formed wood, the course of the various strands of a bundle is not uniform, some going up, some down, and others entering more or less transversely (fig. 11).

It follows necessarily that every cycad which bears terminal cones must have cone domes in the pith. This would include all the living cycads, with the single exception of the ovulate plant of *Cycas*, in which the sporophylls are borne in a loose crown like the foliage leaves, and the growing point is not transformed into a cone, but remains meristematic. It is possible that in specimens of *Encephalartos*, which produce several cones in a circle, the meristem remains as in *Cycas*. In such a case, no cone dome would be formed; but if at any time such a plant should produce only one cone, or two or more cones in a cluster, a dome would be formed.

In *Macrozamia Fraseri*, WORSDELL (6) found numerous bundles in the pith, but claimed that they had no relation to cones. This species usually bears only a single cone, and consequently must have cone domes in the pith. It is possible that WORSDELL'S plant, being a greenhouse specimen, may never have produced a cone, but *Dioon edule*, which elongates very slowly, may show as



FIGS. 12–14.—*Dioon spinulosum:* fig. 12, longitudinal section of mature wood, showing apparently compound nature of the large ray at the upper portion, the bundle at the middle, and mucilage duct lower down; the dark spots are calcium oxalate crystals; fig. 13, longitudinal radial section; fig. 14, transverse section; all ×25.

many as three cone domes in a single transverse section of the trunk, and the arrangement of pith bundles resembles that described for *Macrozamia*. Since the question would be settled by a glance at a longitudinal section of a cone-bearing *Macrozamia* trunk, it is hardly worth while to speculate.

HISTOLOGICAL STRUCTURE

The living trunk of *Dioon spinulosum* cuts rather easily with an ax or machete, but is amazingly difficult to saw. Microtome sections of fresh material are not hard to cut, but transverse and longitudinal sections are likely to break at the large fragile medullary rays. A general view of the histology of the wood is shown in figs. 12–14.

XYLEM.—The xylem, in the older parts of the stem, consists principally of very long tracheids, and is traversed by large and small medullary rays.

Some writers state that there is no protoxylem in the adult cycad trunk, but the statement obviously rests upon a mistaken notion as to the character of protoxylem, such writers assuming that only spiral and annular vessels should be entitled to the name, instead of applying the term to the first xylem differentiated in a bundle, without respect to the character of the markings on the cell walls. The adult stele of *Dioon spinulosum* is endarch, and the protoxylem consists of scalariform tracheids which pass gradually into the pitted tracheids with pointed ends, constituting the principal mass of the xylem. The transition is unmistakable, the scalariform markings, elongated pits, and typical bordered pits sometimes being found in a single tracheid. The bordered pits are multiseriate, two, three, and even five or six rows being found in a radial view of a tracheid, so that in radial sections the wood might be mistaken for that of *Araucaria* (fig. 15). Pits are occasionally found on the tangential walls, but they are not numerous and are irregularly scattered.

Besides the tracheids with pointed ends, the xylem contains elongated cells with transverse walls (figs. 12 and 15–17). These at first are thin-walled and contain starch, but later may or may not become lignified and pitted. They are not uniform in length or constant in position, although they are most numerous in contact with the medullary rays (fig. 12). That their origin is the same as that of the ordinary pitted tracheid is seen at once in a transverse section of the wood (fig. 17).

Still another form of tracheid is found in the large medullary rays (fig. 18). These tracheids are scalariform, are irregular in outline, and are nearly erect at their upper end, but become nearly horizontal deeper down in the ray, so that a tangential section of the ray shows them in both longitudinal and in transverse section. Every large medullary ray would show these peculiar tracheids at some point or other, and they are particularly numerous near the pith. They connect the leaf trace bundle, which is found in every large ray, with the secondary xylem, a connection hitherto unknown in cycads. Such a secondary connection of the leaf trace is a prominent feature in angiosperms. Professor R. B. THOMSON examined preparations of the large medullary rays, and

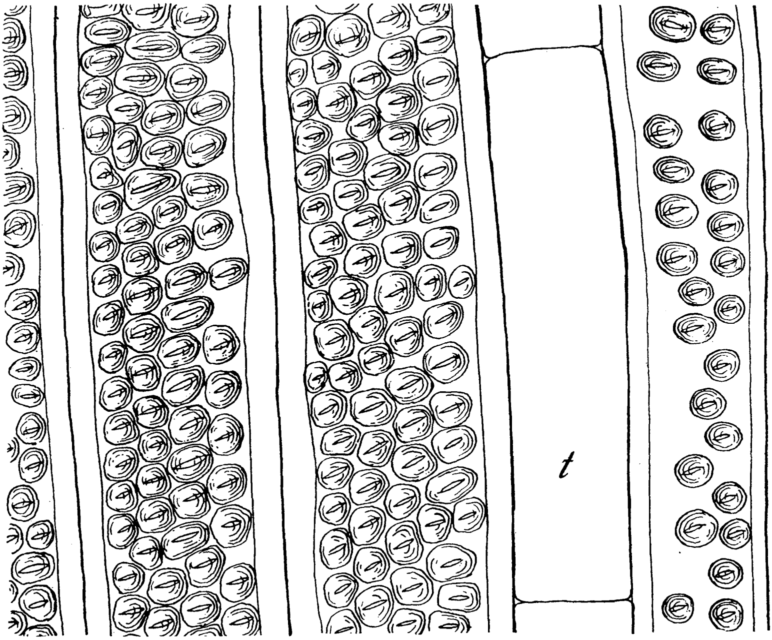
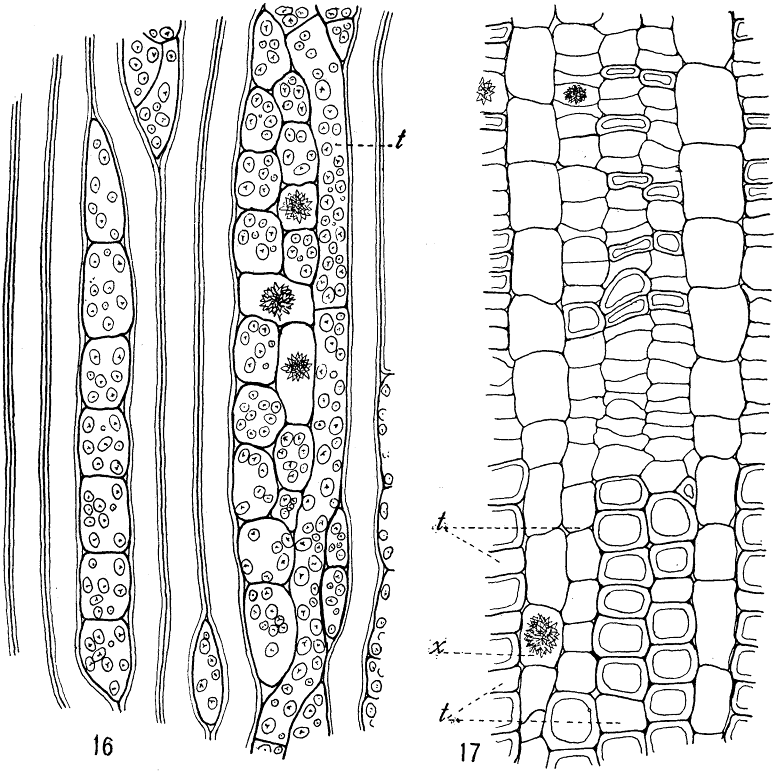


FIG. 15.—*Dioon spinulosum:* longitudinal radial section of mature wood showing multiseriate bordered pits, and also one of the thin-walled cells (*t*) of the xylem; ×390.

I am indebted to him for the suggestion in regard to their connections.

The growth rings, to the naked eye, appear almost as distinct as in dicotyls, but under the microscope they are not so conspicuous (figs. 19 and 20). The latter figure presents one of the most conspicuous rays which could be found. In *Dioon edule*, the rings appear about the same to the naked eye, but under the microscope are quite distinct, and seem to differ considerably from those of *D. spinulosum*, as might be expected from the description given in



FIGS. 16, 17.—*Dioon spinulosum:* fig. 16, longitudinal tangential section of mature wood, showing thin-walled cells of the xylem (*t*) containing starch, the xylem tracheids, and the small medullary rays containing starch and calcium oxalate crystals; fig. 17, transverse section showing the phloem with several thick-walled cells, xylem with thick-walled tracheids and several of the thin-walled cells (*t*); *x*, calcium oxalate crystal in medullary ray; both ×125.

connection with the number of rings. I have not yet found time to give them a careful study. In the plant of *Ceratozamia*, already referred to, the cells of the xylem are quite uniform, there being no trace of growth rings, and a similar condition was found in several stems of *Zamia floridana.*

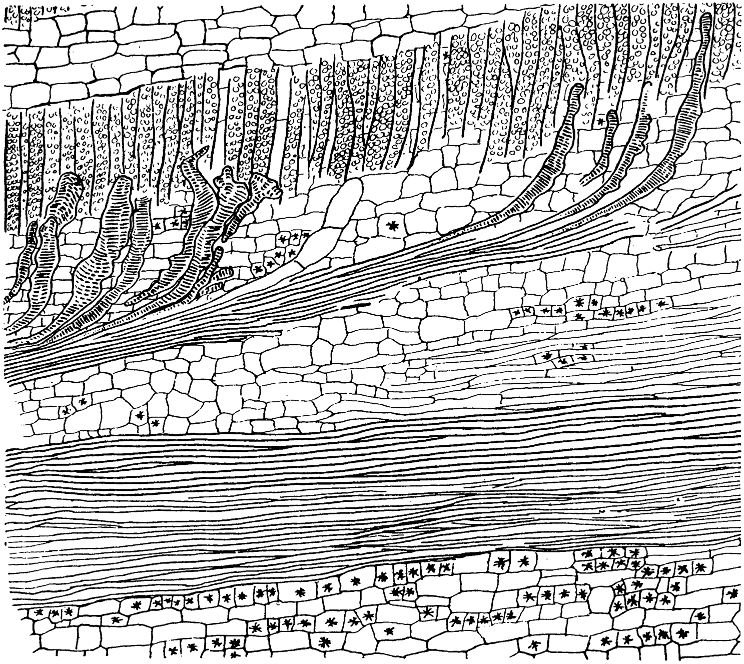


FIG. 18.—*Dioon spinulosum:* portion of large medullary ray, showing the tracheids indicated in tangential section at the tip of the large ray in fig. 12; somewhat above the scalariform tracheids are pitted tracheids of the secondary wood; the lower third of the figure shows part of the leaf trace bundle in the ray; many cells contain calcium oxalate crystals; ×40.

PHLOEM.—The phloem was overlooked by BRONGNIART, doubtless on account of its great extent and the numerous bast fibers which makes it resemble the wood. A small portion of the xylem, the cambium, and a small portion of the phloem of *Dioon spinulosum* are shown in fig. 17. The extent of the phloem is indicated in the photomicrographs (figs. 3, 4, and 8–10). In longitudinal section, especially in tangential section, the resemblance to the wood is even more striking, the medullary rays being just the same, and the bast fibers having about the same arrangement as the long tracheids of the xylem. This structure makes the phloem nearly as rigid as the wood.

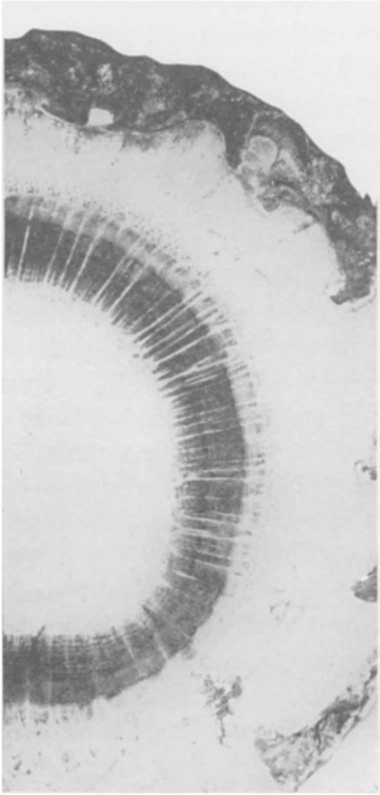


Fig. 19

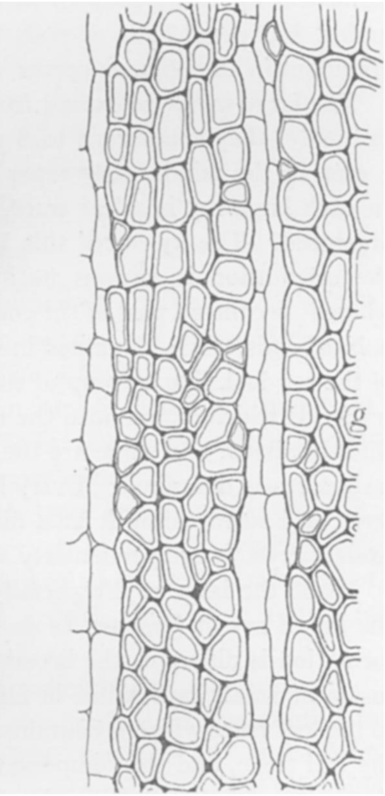


Fig. 20

Figs. 19, 20.—*Dioon spinulosum:* fig. 19, photograph showing growth rings, ×¾; fig. 20, a single growth ring (*g*); ×125.

Rays.—In a transverse section the large medullary rays are as conspicuous as those of *Quercus*, and the small rays, while not nearly so conspicuous, are readily visible to the naked eye (fig. 3).

The small rays vary greatly in longitudinal extent, some showing only a single cell in tangential section, while others may show more than 50, and may reach a width of 3 or 4 cells. The great majority of the small rays are less than 20 cells in longitudinal extent, and are one or two cells wide, often two cells wide in the middle and one cell wide at both ends (fig. 12). Radially, the rays extend from the pith to the cortex, few if any new rays being formed as the trunk grows. Most of the cells contain large starch grains, but some have crystals of calcium oxalate, which is also abundant in the phloem, cortex, and pith.

The large rays also extend from the pith to the cortex. Longitudinally, they measure 4 to 8 mm., and from a width of about 1 mm. in the middle they taper to a single cell above and below. In each large ray is a leaf trace, with its phloem more or less disorganized. The xylem of this bundle is usually uppermost, but the orientation is various until the bundle reaches the cortex, where it becomes a part of the characteristic girdle. From both the pointed ends, tracheids extend into the ray, often making nearly half of the ray look like a group of small rays (fig. 12). Most of these tracheids which extend into the rays are scalariform, but some are slightly pitted, and some are the cells of the wood with transverse walls already described. Every large ray has at least one mucilage duct, and surrounding it at a distance of a few cells, the calcium oxalate crystals are particularly abundant.

While the large ray, especially in tangential section, resembles the broad ray of *Quercus*, as described by EAMES (**9**), its mode of formation is different, the broad ray of *Quercus* originating by the fusion of small rays, while in *Dioon* the broad ray owes its origin to the leaf trace which it contains. The tissues simply grow around the leaf trace, and the compound appearance of the ray, shown at the upper end of the photomicrograph (fig. 12), is a secondary, not a primary feature.

COMPARATIVE HISTOLOGY.—The trunks of *Dioon spinulosum*, *D. edule*, *Ceratozamia mexicana*, and *Zamia floridana* have some histological characters in common, and it is probable that all the Cycadales have enough histological peculiarities to identify the order by the structure of the trunk. The four species mentioned above are easily distinguished from each other by such histological characters, but it is very doubtful whether nearly related species of a large genus like *Zamia* could be so distinguished from each other. The distinction would doubtless be much more difficult in young trunks than in old ones.

The structure of the trunk of *Dioon spinulosum* is remarkably like that of the Bennettitales. The growth rings resemble those of *Cycadeoidea Jenneyana*, as described by WIELAND; the phloem, with its numerous thick-walled fibers in transverse section, is very similar to that of *Cycadeoidea Wielandi;* and the xylem, as it abuts upon the pith, also resembles that of *Cycadeoidea*. But there are also contrasting features; the broad medullary rays are not figured in the Bennettitales, and in the xylem cells with transverse walls seem to be lacking.

Summary

1. The paper deals with field material of adult stems of *Dioon spinulosum*, *D. edule*, *Ceratozamia mexicana*, and *Zamia floridana*, particular attention being given to *Dioon spinulosum.*

2. In *Dioon spinulosum* the xylem zone in a plant 6 meters in height reaches a width of 10 cm., far exceeding the extent of any xylem zone previously described for any cycad.

3. *Dioon spinulosum* and *D. edule* have growth rings, which in *D. spinulosum* correspond to the periods of activity which result in the formation of crowns or cones, but which in *D. edule* do not correspond to such periods. No growth rings were found in *Ceratozamia mexicana* or *Zamia floridana.*

4. Cone domes in the pith were studied in the four species.

5. The histological character of the adult stem was studied in *Dioon spinulosum.* The protoxylem consists of scalariform tracheids, from which there is a gradual transition to the tracheids with multiseriate bordered pits, constituting the principal part of the wood. There are also cells with the same origin as the pitted tracheids, but with transverse walls which may remain thin-walled and contain starch or may become lignified. Besides the leaf trace bundles, scalariform tracheids are found in the large medullary rays.

6. Both in the general appearance of the transverse section and in histological characters the adult trunk of *Dioon spinulosum* resembles that of *Cycadeoidea.*

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